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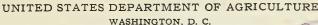
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PARASITIZATION OF THE MEDITERRANEAN FRUITFLY IN HAWAII, 1914–33

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CONTENTS

	Page		Page
Introduction Manner of obtaining data Records of parasitization Interrelations of the parasites. Effect of host fruit on parasitization of fruitfly larvae	2 3 9	Effect of host fruit on parasitization of fruitfly larvae—Continued. Parasitization in larvae from coffee cherries. Records of infestation. Summary. Literature cited.	12 13 16

INTRODUCTION

The Mediterranean fruitfly (Ceratitis capitata Wiedemann) was first observed in the Territory of Hawaii in 1910. Owing to a favorable environment it increased rapidly in numbers, and within 3 years was well established on all inhabited islands of the Hawaiian group. Its presence made necessary quarantine restrictions forbidding the entry of Hawaiian-grown fruits and vegetables into the mainland of the United States in order to prevent the spread of the insect to the vast semitropical fruit-growing areas of the country. This closing of the principal export market for Hawaiian produce was a serious detriment

to the horticultural development of the islands.

The importance of this fly as a pest of tropical and subtropical fruits was realized at the time of its discovery in Hawaii. Entomologists of both the Federal and Territorial Governments began immediately to study its reaction to its new environment in an attempt to develop effective control measures. Eradication of the fly by collecting and destroying all host fruits was first attempted. This work was carried on for about 3 years, when it was abandoned as futile owing to the abundance and wide distribution of host fruits. The fly is capable of developing in Hawaii in at least 75 varieties of host fruits, many of which grow in inaccessible locations in wild or mountainous areas. During the period 1912 to 1914 spraying experiments with poisoned baits were conducted, but these proved of little value as control measures. Trapping adults by using attractive baits failed as a control measure, since kerosene oil was the only attractant known at that time, and practically all flies caught in the kerosene traps were males.

The rapid spread of the Mediterranean fruitfly when it first arrived in Hawaii was due not only to an abundance of host fruits and a favorable climate, but also to the absence of natural enemies. No parasites and few predacious enemies were present. Of the latter, the ant *Pheidole megacephala* F. was the only one of importance. This

species is far more abundant than any other ant in Hawaii, being found in large numbers in all fruit-growing areas. Its food is largely animal matter, and it voraciously attacks insects whenever they are available. Observations have shown $(7, p. 464)^1$ that it may destroy from one-third to four-fifths of all fruitfly larvae in certain fruits that have fallen to the ground. To overcome the rapid increase of the fly and its resulting damage to horticulture the policy was adopted by the Territorial government of importing natural parasites from localities where the fly had long existed.

Parasites of the Mediterranean fruitfly were first introduced and established in Hawaii in 1913 and 1914. Of the successful introductions, there were three species of Braconidae of the subfamily Opiinae, viz, Opius humilis Silv. and (Diachasma) O. fullawayi Silv. from South Africa, and (Diachasma) O. tryoni Cam. from Australia; and one species of Chalcidoidea belonging to the family Eulophidae, Tetrastichus giffardianus Silv., from South Africa. Of several other species of parasites introduced only one, the pupal parasite Dirrhinus giffardi Silv., has been recovered, but it has not become sufficiently numerous

to be a factor in the control of the fruitfly.

The first liberation of fruitfly parasites on the island of Oahu was a colony of Opius humilis released in December 1913. Approximately 6 months later, in July 1914, numerous adults of this species were being reared from larvae in fruits collected about Honolulu. O. tryoni, O. fullawayi, and Tetrastichus giffardianus were first liberated about Honolulu during the last 3 months in 1914, after O. humilis had become well established. Many more colonies were liberated during 1915, and in June of that year small numbers of adults of these three species were recovered. From that time on, they increased in numbers until Mediterranean fruitfly larvae from almost any infested fruit The Hawaii laboratory of the Bureau would produce some parasites. of Entomology, United States Department of Agriculture, has recorded for the 20 years 1914-33 the parasitization of the fly in various host fruits about Honolulu by each of these four species. Since 1916, in connection with these records, the average infestation per fruit by the fly in its various host fruits has also been recorded. The results of these observations, 1913 to 1924, inclusive, have already been published (1, 3, 4, 6, 8, 9, 10). The records for the period 1925-33 are included in this circular, the object of which is to record the efficiency of each species of parasite for the 20-year period 1914-33, as well as to show variations in the average infestation per fruit for each year from 1916 to 1933.

MANNER OF OBTAINING DATA

An explanation of the methods used in obtaining records of parasitization necessitates a few remarks on the biology of the Mediterranean fruitfly and the parasites under consideration. The egg and larval stages of the fly are passed within the host fruit. When the larvae are fully grown they usually leave the fruit, drop to the ground, and pupate in the soil or beneath rubbish; but occasionally pupation may take place inside fallen and dried fruits. All four species of parasites

¹ Italic numbers in parentheses refer to Literature Cited, p. 17.
² In 1915 Gahan (2) suppressed the generic name Diachasma Foerster as a synonym of Opius Wesmael. Previous publications on parasites of the Mediterranean fruitfly in Hawaii have considered tryoni and fullawayi as species of Diachasma, but in view of Gahan's suppression of Diachasma the generic name Opius is used throughout this circular.

attack the host larva when it is over half grown, and while it is still within the host fruit, either on the tree or after it has fallen to the ground. The three opine parasites attack the fruitfly by puncturing the skin of the host fruit with the ovipositor and inserting an egg within the host larva. It is necessary, however, for the small parasite Tetrastichus giffardianus to obtain entrance to the fruits through a crack or other opening, where it locates the fly larvae and oviposits

Although the parasite eggs usually hatch within the host larva, the parasites do not cause its death until it has formed the puparium. Development of a parasitized fly ceases shortly after the puparium is formed, and the greater part of the larval stage and all of the pupal stage of the parasite are passed within the host puparium. Consequently, accurate percentages of parasitization may be secured by obtaining puparia of the fly and counting the emerging adult flies and parasites. In the case of parasitization by Tetrastichus gifardianus, however, 8 to 10 adult parasites may represent only one host. (7, p. 452.) All records of parasitization by this species over the 20-year period under consideration were therefore computed on the basis of 10 adults from 1 host pupa.

Puparia for parasitization counts were obtained from almost daily collections of fruits in Honolulu and environs. The fruits from each collection were counted and placed in wire-bottom trays over clean ocean sand. After the larvae became full grown they emerged from the fruit and dropped into the sand to pupate. The resulting puparia were sifted from the sand three times weekly and held in rearing jars

until all adult flies and parasites had emerged.

Under normal conditions, the fruitfly larvae in fruits remaining on the tree or lying on the ground are exposed to parasitization until they are full grown and leave the fruit to pupate. Larvae in fruits collected for parasite records, however, were not exposed to parasitization after they were collected and placed in the insectary. Therefore, to obtain parasitization percentages as nearly comparable with those occurring under field conditions as possible, records were made only from those larvae leaving the fruits during the first 2 to 6 days after collection. Well-developed larvae remain in some fruits longer than in others, and in cases where too few larvae for a representative parasitization record emerged and pupated during the first 2 days of holding, those emerging over a longer period up to 6 days were used. Counts of the number of flies and parasites emerging from each collection of pupae were made, and these furnished the data for determining the parasitization records used in the following section.

RECORDS OF PARASITIZATION

The percentages of parasitization accomplished by each species of parasite on fruitfly larvae in all fruits collected over monthly periods during each year from 1914 to 1933, inclusive, are recorded in table 1. The host fruits from which these records were secured were all collected on the island of Oahu, except samples of coffee cherries (coffee berries) that were collected once each year, except in 1919, 1920, 1921, 1925, and 1930, in the Kona district on the island of Hawaii. Almost daily collections of fruits for parasitization records were made on the island of Oahu throughout the 20-year period. The records presented in this table were compiled from counts of flies and parasites reared

Table 1.—Parasitization of the Mediterranean fruitfly in Hawaii by each species of parasite and by monthly periods. Records are from all fruits collected during the period 1914-33

6601	1931 1932 1933 Mean	Per- Per- Per- Per- cent cent cent cent 3.5 6.1 9.9 8.6 7.0 11.3 36.6 11.5 0 0 0 2.6 2.7 0 3.6 4.7 4.7 4.7 4.7	13.2 17.4 46.8 32.4	12.0 9.9 18.7 11.3 2.9 0.0 0.0 1.6 3.8 0 2.2 4.4 4.4	18.7 27.8 38.5 29.5	27.7 2.1 16.4 4.2 10.6 1.5 4.7 0 2.7 1.8 .3 1.7 4.2	32.1 27.7 11.1 31.7	35.4 5.6 42.6 20.3 11.6 15.1 18.5 13.1 0 0 0 1.0 9.4 .2 1.6 2.5	56.4 20.9 62.7 36.1	25.0 1.6 5.5 13.9 4.3 7.9 5.3 19.6 0 0 0 .6 8.9 .6 .5 1.9	38.2 10.1 11.3 34.9	11.6 8.2 22.0 20.3 11.6 0.0 0 0 0 1.7 3.5 3.5 3.5	
-	1930	Per- cent 8. 2 11. 7 0 1. 1	21.0	9.4 6.7 0 2.6	18.7	18.5 18.1 0 7.0	43.6	35.3 0 0 1.6	40.2	10.2 3.5 0 1.0	14.7	11.6 7.5 9.2	
-	1929	Per- cent 9.5 9.5 35.0 0	3 48.2	8.6.2.6	3 32.8	10.0 18.0 18.0 4 3.1	31.2	9 11.8 0 31.8 0 4.	7 33.6	30.03	39.3	19.9	
	1928	Per- cent 4.5 16.0 0 0 14.8	9 25.3	27.10.0	6 38.8	1 2 2 3.3 4 4 7 4.4 4.4	4 11.6	0 8.0	4 17.7	0 8.8 6 19.1 9 1.0	5 29.2	19.4	
-	1327	Per- cent 2.4 20.2 1.1	23.8	36.5	47. (31.2	38.	1.0 H	27.	0.62	30.5	5.3 21.2 1.9	
1000	1920	Per- cent 22. 0 26. 6 11. 8 6. 5	6,99	10.7 7.8 14.2	32.7	38.1	41.4	2. 5. 6. 6. 6. 6. 6. 6. 6. 6. 6. 6. 6. 6. 6.	51.2	26.9 12.2 1.7	41.1	14.3 14.6 5.3	
7-05 Togr	1920	Per- cent 4.4 4.4 6.6	15.9	4. 3. 4.	14.8	20.02	10.0	0.00	12.8	18.5	23.1	12. 2 24. 6 24. 6 . 1	
period 1914-09	1924	Per- cent 9.3 23.9 1.7	35.6	26.2 14.1 2.9 2.9	44.6	25. 9 22. 7 7. 1 2. 9	58.6	28.7	37.7	15.9	22.8	8.3 0.7	
1033	1923	Per- cent 1. 2 20. 5 15. 1	37.2	8.3	15.1	12.1	24.5	3.52	25.1	21.2	26.3	12.9 1.1 8.6	
	1922	Per- cent 1. 4 8. 9 1. 8 1. 8 26. 6	38.7	10.5 7.0 1.5 9.4	28.4	12.8 9.6 2.0 7.9	32.3	16.0 15.0 .9 .0	37.9	14. 2 39. 3 1. 2	55.2	1.2 48.7 3.6 4.0	
1001	1321	Per- cent 9. 6 26. 9 7. 6 6. 2	50.3	15.7 13.3 9.8	41.5	4.0 5.7 4.0 13.9	27.6	0.94-1.9	15.8	17.8 54.3 1.6 2.9	76.6	16.8 27.9 5.6 10.5	
toro 1000 1001 100	1920	Per- cent 6.7 5.2 12.4 4.8	29.1	10.6 7.7 4.4 16.0	38.7	23.6 22.7 8.7 10.9	45.9	15.0 5.9 2.6 8.2	26.3	19.4 26.4 1.3 2.7	49.8	24.8 14.4 1.2	
2010	1919	Per- cent 6.8 17.1 2.4 2.4	27.2	19.4 11.8 1.9 2.4	35. 5	7.7 7.7 1.0 2.2	18.5	13.3 13.3 8.0	26.4	38.8	46.9	34.3 1.3 1.3 6.2	
9191	1918	Per- cent 4.8 9.6 6.2	21. 4	25.53	6.6	24.1	37.5	10.3 27.8 5.0 4.	43.5	16.5 17.3 2.0	36.0	11.8 48.6 .8	
1	1917	Per- cent 39. 0 15. 6 2. 0 2. 0 2. 4	59.0	20.0 3.8.6 1.3.0 1.3.0	32.9	27. 1 22. 5 12. 6 12. 6 1. 3	63. 5	9.0 27.6 5.5 1.2	43.3	26.8.8	40.9	11.7	
9101	1916	Percent 5. 5 . 4 . 1. 0 1	7.0	17. 6 1. 7 0	19. 5	13.7 . 2 . 6	14.7	34.8 2.1 .7 .04	37.6	19.6 6.1 .9 .09	26.7	7.8 15.5 4.5 .009	
1	1915	Per-						69.4	69.4	44.1	44.1	20.8	
1	1914	Per- cent (i)											ĺ
34	Month and parasite	January: Opius humilis O tryoni O fultwoaji Tetrastichus giffardianus.	Total	February: O hamilis O tryoni O, fullawayi T, giffardianus	Total	March: 0. humilis 0. fullowi 0. fullowayi T. giffardiunus	Total	April: O humilis O trijoni O fullawayi T. giffardianus	Total	May; O humilis O tryoni. O fullawayi. T. giffardianus.	Total	June: O humilis O trigoni. O fullawayi. T. giffardianus.	

		MEDIII									
10.8 21.1 2.0 6.7	39.1	7.6 21.1 2.5 9.6	39.1	9.8 18.6 2.8 11.8	41.3	10.9 20.7 3.6 8.7	42. 2	13.4 20.7 4.6 10.0	48.6	11.2 19.7 6.7 7.9	45.5
25. 0 19. 4 0	44.9	12. 5 19. 8 0 4. 3	36.6	19. 1 32. 9 0 10. 3	62.3	24.8 47.0 0 6.2	78.0	32.0 37.5 0 9.1	78.6	34. 7 4. 1 0	39.6
10. 7 19. 1 0 5. 1	34.9	8.0 18.2 0 5.1	31.3	5.7 0.7 9.8	16.2	27.3 9.7 1.7 3.7	42.4	43. 1 29. 6 0 4. 6	77.3	17. 2 38. 7 0	56.8
9.3 12.6 0 8.6	30.5	16.5 29.1 0 1.1	46.7	14.5 7.5 0 3.4	25. 4	2.4	10.6	4.0 14.3 0	18.7	8.5 6.1 1.4	16.0
9.9 12.8 0 12.9	35.6	9.7 5.3 5.6	20.6	10.2 5.8 0 2.4	18.4	4.1 2.0 2.2	8.3	8.3 0.9 13.0	30.1	20.9 15.1 0	36.0
20.8	32.8	7.6 27.6 0 3.1	38.3	10.1 20.3 0 10.2	40.6	8.8 37.5 0 8.7	55.0	2.9 34.2 0 13.1	50.2	8.2 18.0 0 7.5	33.7
10.9 15.2 0 3.5	29. 6	16.3 20.0 0 4.5	40.8	11.2 13.1 0 3.9	28.2	7.0 14.1 11.4 3.6	36.1	7.4 14.9 0 3.0	25.3	9.3 17.6 0 6.8	33.7
9.6 13.6 0 8.8	54.0	3.1 40.5 2.9 3.7	50.2	5.3 37.3 0 5.1	47.7	13.3 26.3 3.1 11.3	54.0	9.4 25.6 0 8.1	43.1	4.8 40.2 0 6.9	51.9
3.4 6.6 7.2	17.7	1.4 10.9 20.4	32.8	3.4 8.1 20.1	32. 2	12.3 8.2 1.4 5.0	26.9	17.8 1.1 0 2.7	21.6	12.3 5.0 0 6.3	23.6
13.8 15.1 1.0	30.0	18.3 25.5 .1 3.6	47.5	18.1 12.7 9.2	40.3	17.5 14.1 1.5 11.6	44.7	14.3 13.1 .1 15.3	42.8	25.9 32.9 0 8.0	8.99
3.3 47.6 .3	52. 1	25.9 25.8 2.0	33.8	17. 2 25. 1 9. 9	52. 4	16.9 20.6 1.6 5.9	45.0	11. 6 14. 5 15. 8 20. 4	62.3	18.3 41.9	61.0
7.1 4.7 11.3	23. 5	2,7 12,7 1,0 19,3	35.7	6.1 7.2 1.5 51.4	66.2	5.8 4.5 1.0 60.2	71.5	16. 2 24. 4 5. 9 16. 5	63.0	3.7 16.7 0 18.4	38.8
1.9 13.7 5.4 15.4	36.4	20.4 3.1 6.8	31.3	1.8 21.4 1.7 6.1	31.0	1.9 58.0 5.8	0.99	37.6 9.5 5.4	54.8	2,4 34.0 1.2 18.6	56.2
3.6 27.3 5.3 19.5	55.7	5.8 21.4 4.1 39.4	70.7	26.2 33.2 33.2	70.7	2.0 22.6 12.4 7.4	44.4	3.0 18.9 6.5 20.1	48.5	4.7 14.0 2.4 30.3	51.4
5.2 28.9 16.0 7.8	57.9	8. 7 13. 7 24. 1 10. 5	57.0	4.8 22.7 22.7 20.4	75.1	2.0 46.8 8.5 7.1	64. 4	1. 7 26. 1 17. 3 15. 6	60.7	4.4 9.7 18.4	33.0
22.0 28.9 1.0 8.1	0.09	7.4 8.3 1.0 25.5	42.2	13.8 3.0 7.9	30.1	6.5 11.7 2.6 6.1	26.9	6.9 21.1 1.6 8.4	38.0	11.6 33.5 9.9	55.6
52.2 3.6 3.6	59.9	38.1 3.8 7.9	50.5	28.0 3.4 13.3	47.1	6.5 22.0 3.2 9.4	41.1	25.3 21.7 11.2	58.7	21. 5 37. 7 10. 9	70.5
3.9 26.6 19.6	51.0	16.4 16.4 19.2	33.1	5.2 31.3 13.2 2.7	52. 4	7.2 16.4 13.2 8.4	45.2	17. 2 22. 6 11. 6 20. 9	72.3	5.3 16.7 5.2	27.9
3.7 13.0 1.8 .02	18.5	8.8 27.0 .9	37.5	9.7 34.0 1.1	45.2	13.8 27.4 1.7 1.4	44.3	11.0 25.2 6.7 1.4	44.3	13. 3 5. 3 4. 6	44.1
26.8	28.0			32.5 .3 0 4.0	36.8	25. 0 1. 9 4. 5	32. 2	20.4 1.4 11.3 0	33.1	6.8 61.2 0	68.2
29. 4	29.4	7.3	7.3	8. 4	8.4	7.2	7.2				
July: O humitis O trigoni O trigoni T giffardianus	Total	August: O humitis O trigoni O trigoni O fullowayi T, giffardianus	Total	September: O humilis O tryoni O tryoni O tryoni T, giffardianus	Total	October: O humitis O tryonic O tryonic O tryonic O tryonic O tryonic	Total	November: O humilis O tryoni O tryoni O tultawayi T giffardianus	Total	December: O humitis O tryonic O tryonic O tryonic O tryonic O fultanayi	Total

¹ No records are indicated for the periods before the parasites had time to become established or when no host fruit collections were made. The mean in the final column covers only those periods for which there are records.

from large numbers of host fruits, representing 40 different varieties. From 95,000 to 150,000 fruits, with an average of approximately 110,000, were collected annually for this purpose. In view of the large numbers of fruits and larvae under observation the percentages of parasitization in the table are believed to be fairly representative of those actually occurring in the field. However, owing to the fact, as stated above, that larvae held for parasite records were exposed to parasites from 2 to 6 days less than those remaining in the field, the percentages of parasitization in the table are probably slightly lower than those in larvae in uncollected fruits. More detailed information on methods of securing data may be found in previous publications

already cited.

The data in table 1 give a detailed record of the development and progress of each of the insects in parasitizing the fruitfly during the first 20 years of parasite work in Hawaii. The percentage of parasitization by each species during each month is shown, as well as the means for the entire period and the total parasitization for each month. In figure 1 is shown graphically the monthly trend of parasitization by each species and the relation of the species to one another during the various months of the year. Opius humilis is shown to be the most abundant parasite in March and April. It reaches its highest efficiency when the other three species are practically at their lowest in effectiveness. During the other months of the year O. tryoni is more abundant than O. humilis, reaching its maximum of effectiveness in July and August. Varying numbers of O. tryoni and O. fullawayi are known to hibernate in the full-grown larval stage within the puparium of the fly (7, pp. 428, 431, 446) during the cooler months of the year, owing no doubt to the habits of the parasites in the more temperate climate from which they were introduced into Hawaii. This habit accounts largely for the decline in numbers of O. tryoni during the early months of the year and the proportionate rise in numbers of O. humilis, as shown in the graph. As high as 50 percent of the larvae of O. tryoni in some samples have been observed to remain in a state of hibernation from 2 to 7 months. During the warmer months of the year hibernation occurred in less than 1 percent of O. tryoni under observation. Adults of O. tryoni and O. fullawayi reared from hibernating larvae and emerging later than 1 month after fruits were collected were not used in compiling data in table 1 and figure 1, consequently the field parasitization by these two parasites would be slightly higher than that shown.

Table 2 records the parasitization by each species in each year from 1914 to 1933, inclusive, together with the total for each year. Variations in effectiveness of each species from year to year are shown. The table shows Opius tryoni to be the most effective parasite, with O. humilis, Tetrastichus giffardianus, and O. fullawayi as second, third, and fourth, respectively, in importance. During the 20-year period under review, each parasite reached its maximum efficiency as follows: O. humilis in 1915, O. tryoni in 1918, O. fullawayi in 1920, and T. giffardianus in 1923. The unusually high parasitization by T. giffardianus in 1923 is due to an abnormal increase in numbers of this parasite in a small area from which large numbers of Indian almonds were collected (10, p. 9). The data on annual percentages of parasitization by each of the four introduced parasites are shown graphi-

cally in figure 2.

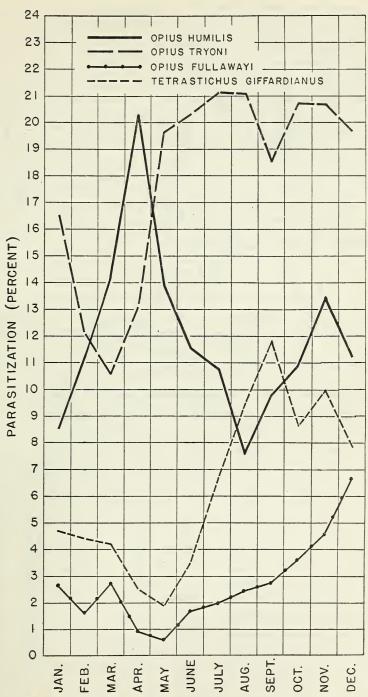


FIGURE 1.—Mean monthly percentage of parasitization of the Mediterranean fruitfly in Hawaii during the period 1914-33.

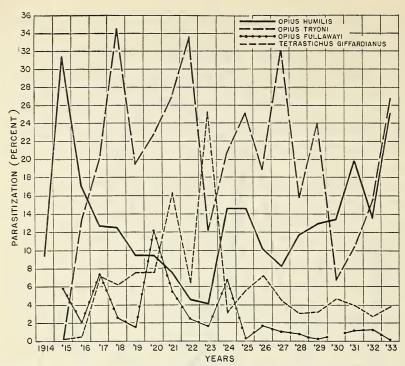


FIGURE 2.—Percentage of parasitization of the Mediterranean fruitfly in Hawaii by years by the four introduced parasites, 1914-33.

Table 2.—Parasitization of the Mediterranean fruitfly in Hawaii over yearly periods, 1914-33

			Pa	arasitization l	by—	
Year	Fruitfly larvae			Opius fullawayi	Tetrasti- chus gif- fardianus	Total
1914	Number 32, 553	Percent 9, 4	Percent	Percent	Percent	Percent 9.4
1915 1916 1917 1918 1919 1920 1920 1922 1923 1924 1925 1926 1927 1929 1929 1929 1930 1930	28, 010 83, 340 72, 139 63, 480 57, 406 58, 616 58, 562 36, 191 27, 262 30, 134 18, 605 26, 488 12, 209 22, 984 20, 604 14, 322 15, 846 27, 153	31. 5 17. 22 12. 7 12. 4 9. 4 9. 4 9. 4 4. 6 4. 1 14. 5 10. 1 8. 2 11. 9 13. 5 19. 8 11. 9	0.3 13.3 20.3 34.6 19.6 22.7 26.7 26.7 25.2 20.7 25.2 20.7 25.2 18.9 32.0 15.9 10.2	5.9 2.1 7.3 2.6 1.6 12.1 5.5 5.5 2.6 6.8 .2 1.6 1.1 8	0. 2 6 2 7. 2 6. 2 7. 6 7. 7 16. 4 25. 3 3. 1 5. 7 7. 1 4. 4 3. 1 3. 1 3. 2 4. 7 3. 9 2. 8 3. 9	37. 0 33. 2 47. 5 55. 8 38. 2 51. 9 56. 4 47. 2 45. 1 45. 6 37. 7 45. 7 31. 4 40. 4 24. 9 35. 2 55. 7
Average		13. 1	20. 0	2.9	6.3	42.3

In the column representing parasitization by Opius fullawayi in table 2 it is interesting to note the scarcity of this parasite during the

last 9 years of the period covered. Records already published (4, 6, 8, 9, 10) show that O. fullawayi parasitized fruitfly larvae in a wide variety of host fruits during the first 9 years after its liberation in Hawaii. They also indicate its preference for larvae in some host fruits over larvae in others. Its special choice of larvae in coffee cherries, strawberry guava, loquat, and yellow-oleander would indicate some special attraction in these fruits. Since 1924, however, O. fullawayi has been reared in very small numbers and from fruitfly larvae in only a few varieties of host fruits, with the exception of coffee cherries; and during each of the years 1925 and 1926 it was reared from larvae in only 7 other varieties of fruits, and in 1927, 1928, 1929, and 1930 from 11, 2, 1, and 3 other varieties, respectively. With the exception of larvae from coffee cherries, 55,050 fruitfly larvae under observation produced only six adults of O. fullawayi during 1928, 1929, and 1930; while during 1931, 1932, and 1933 no adults of this parasite were reared from 54,536 larvae. During every year since its establishment in Hawaii it has parasitized larvae in coffee cherries in good numbers. The causes are not known for its apparent preference, as compared with other species, for larvae in certain fruits, particularly coffee cherries, and for its later restriction in attack to larvae in coffee cherries only.

INTERRELATIONS OF THE PARASITES

The oviposition habits and process of development of the three opiine parasites *Opius humilis*, *O. tryoni*, and *O. fullawayi* are almost identical. They all oviposit within the well-developed host larva before it leaves the fruit to pupate. The egg, larval, and pupal stages of all three are similar, and are passed within the larvae and pupae of the host. Moreover, only one of these parasites is able to develop in a single host larva. Although only one egg is normally deposited in each host, it is not uncommon to find several parasite eggs in one larva in one of the fruits in which a high percentage of the fruitfly larvae are parasitized. These eggs may all be from one species of parasite, or they may represent the oviposition of two or three species.

Since each fruitfly larva contains food material sufficient for the development of only one individual of the opine parasites, any excess numbers of parasite larvae must be eliminated. A conflict therefore occurs among the newly hatched larvae which nearly always results in the elimination of the Opius humilis larvae when either tryoni or fullawayi is also present. Studies of the interrelations of these parasites in Hawaii (\bar{b}) show that in such cases of multiple parasitism one species may have some influence on the development of another. Although O. humilis was introduced first and became well established before the liberation of either of the other species, its effectiveness steadily decreased from 31.5 percent parasitization in 1915 to 4.1 percent in 1923, after the appearance of O. tryoni and O. fullawayi. As shown in figure 2, humilis reached its peak of fruitfly parasitization in 1915, the year following the first liberation of tryoni and fullawayi. In every year since then, except 1916, 1930, and 1931, O. tryoni has demonstrated a superiority over O. humilis in ability to parasitize fruitfly larvae in competition with the other parasites.

Just how much multiple parasitization retards the development of *Opius humilis* is not known, although the records indicate that under

certain conditions, tryoni or fullawayi may, to a considerable extent, retard the development of humilis when they occur in the same host larva. In fruits such as coffee cherries where the percentage of parasitization by the three species of Opius is high, multiple parasitization occurs often (5). O. humilis has apparently been eliminated from the Kona coffee section on the island of Hawaii, where in 1915 it parasitized 59.4 percent of the fruitfly larvae in coffee cherries (table 5). The fact that it decreased rapidly in effectiveness, as tryoni and fullawayi increased, strongly indicates that their influence was the

The retardation of *Opius humilis* by tryoni and fullawayi is further shown by the variation in efficiency of the parasites in certain months of the year, and follows very closely the changes in abundance of tryoni and fullawayi. During the cooler months of every year, as the numbers of these two are decreased by their hibernation habits, their suppression of humilis naturally decreases. As a result humilis, whose period of development from egg to adult is 3 to 5 days shorter, increases rapidly. The curves in figure 1, representing the seasonal effectiveness of each parasite since the time of their establishment, picture very clearly the interchange in abundance of tryoni and fullawayi combined and that of humilis, due largely to elimination of

the last by the first two.

principal factor in its elimination.

In the case of the chalcidoid Tetrastichus giffardianus, about 10 eggs are usually deposited in each host larva. No cannibalistic tendencies are shown by the young parasite larvae, and all usually develop to maturity. Should an opiine larva be also present, however, a conflict occurs, and several of the chalcidoid larvae are killed, but seldom all of them. The chalcidoids survive the opiine larva by sheer force of numbers and subsequent rapid absorption of the available food. The opiine ultimately dies and one or more of the chalcidoids develop to maturity. Because of the capability of T. giffardianus for surviving the opiines, where both occur together in the same host larvae, this species may be a detriment to the development and increase of the latter (10, p. 9), which have proved more effective in control of the fruitfly in Hawaii.

EFFECT OF HOST FRUIT ON PARASITIZATION OF FRUITFLY LARVAE

Observations on the parasitization of the Mediterranean fruitfly show that the texture of the skin and the thickness of pulp in host fruits influence to a great extent the parasitization accomplished by the three species of Opiinae now in Hawaii. To illustrate this point, in table 3 the total parasitization is recorded for yearly periods for 1924-33 on larvae in seven different fruits. Coffee cherries have a large seed, the skin is easily punctured by the parasites, and the pulp is so thin that every larva within a fruit can be reached by the ovipositor of any of the three opine parasites. Consequently the parasitization of fruitfly larvae in coffee is high. It is not uncommon to find 95- to 100-percent parasitization of larvae in a collection of coffee cherries. In India almonds similar characteristics of the skin and fruit exist, and parasitization of larvae in this fruit is also high, in fact greater than in all others except coffee. The strawberry guava and Chinese orange are small fruits of about the same size, but the former has a very thin skin and soft pulp, whereas the skin of the latter is much thicker and more difficult to puncture. Consequently the

parasitization of larvae in the Chinese orange is nearly always much less than that in strawberry guava. In addition to being more difficult for parasites to puncture, the thickness of the skin of Chinese orange may give the parasites difficulty in locating the host larvae. The West Indian medlar is also a small fruit, but it, too, has a hard covering which the parasites have great difficulty in puncturing. Hence the percentage of parasitization in this fruit is very low even though it is a small fruit with thin flesh and is always heavily infested with fruitfly larvae.

Table 3.—Parasitization of the Mediterranean fruitfly in Hawaii over yearly periods from larvae in some common host fruits, 1924-33

Host fruit	1924	1925	1926	1927	1928	1929	1930	1931	1932	1933
CoffeeIndia almondStrawberry guavaChinese orangeMangoCommon guavaWest Indian med-lar	Percent 63.8 52.4 43.6 12.8 17.2 12.2	54. 1 28. 2 10. 4 17. 2 14. 7	Percent 63. 9 46. 4 17. 5 8. 2 19. 6 23. 1 6. 3	Percent 57. 8 53. 0 39. 7 9. 2 13. 2 15. 0	Percent 21. 8 44. 2 32. 0 5. 3 20. 0 12. 2	43. 8 31. 5 9. 6 18. 7 19. 4	29. 1 52. 8 6. 7 26. 5 9. 0	Percent 39. 8 41. 9 0 3. 6 24. 8 7. 7	Percent 48. 1 42. 6 6. 9 14. 2 4. 0 1. 9	Percent 81. 5 69. 4 63. 7 11. 3 5. 7 5. 1 1. 3

Among the larger host fruits are mangoes and common guavas, which are about equal in size, but the guava is pulpy throughout, whereas the mango contains a large seed covered with a fairly thick pulp. Many fruitfly larvae feed near the center of guavas and keep out of reach of parasites, while the large seed of the mango forces more of the larvae to feed near the surface where they are subjected to parasitization. This condition is reflected in the higher percentages of parasitization of larvae in mangoes, although the tough texture and other qualities of the skin in some varieties of this fruit probably decrease the rate somewhat.

Tetrastichus giffardianus was responsible for only negligible parasitization of larvae in the fruits listed in table 3 during the period covered. In oranges and yellow-oleander fruits, however, it has been much more effective. The combined percentages of parasitization in these fruits by the three species of opine parasites, as compared with the parasitization by T. giffardianus, are shown in table 4. These data indicate that T. giffardianus was much more effective during the period under consideration for these two fruits. Yellow-oleander is a fairly small fruit with a thin tender skin, and the majority of fruitfly larvae therein should be easily within reach of the opine parasites. The comparatively small number of adults of these parasites reared from larvae in this fruit is doubtless the result of their destruction by T. giffardianus, as shown in a previous publication (5, pp. 292–293). The same interference by T. giffardianus has occurred in orange, and this, together with the size of the orange and the thickness of skin, has reduced the effectiveness of the opine parasites even lower than in yellow-oleander.

Table 4.—Parasitization of the Mediterranean fruitfly from larvae in yellow-oleander and orange fruits over yearly periods, 1924-33

Fruit and parasite	1924	1925	1926	1927	1928	1929	1930	1931	1932	1933
Yellow-oleander: Tetrastichus giffardianus. Opiine parasites. Orange: Tetrastichus giffardianus. Opiine parasites.	Per- cent 45. 3 9. 5 22. 6 11. 6	Per- cent 15. 5 18. 5 12. 1 6. 2	Per- cent 13. 2 11. 3 5. 8 11. 7	Per- cent 7.0 9.6 10.4 6.0	Per- cent 8.7 12.5	Per- cent 15. 8 18. 5 13. 9 3. 6	Per- cent 25. 2 9. 5	Per- cent 24. 3 4. 0 33. 7 2. 0	Per- cent 19. 2 16. 4 31. 4 4. 1	Per- cent 7.9 6.4 10.2 11.2

PARASITIZATION IN LARVAE FROM COFFEE CHERRIES

Percentages of parasitization of Mediterranean fruitfly larvae by the three opiine parasites in coffee cherries from the Kona district of the island of Hawaii are shown in table 5. Data in this table are important because they show clearly the progress of each species in an environment where the host larvae, in the predominant variety of fruit, are easily parasitized. This district is approximately 190 miles from the island of Oahu, where Honolulu is located and where the majority of fruits were collected for the parasitization records in this circular. In this coffee-growing area the high degree of parasitization of larvae in coffee by introduced parasites of the Mediterranean fruitfly has decreased the fly population until most host fruits are free from infestation and only slight infestation is found in others. Coffee cherries were collected each year during August, September, or October, during the years 1914–33, except 1919, 1920, 1921, 1925, and 1930, for parasitization records. Samples were taken from the same locations in an area approximately 10 miles long and 1 mile wide. From 1923 to 1933, inclusive, excepting 1927, collections averaged 20,000 fruits each year collections were made. The records for 1927 are from 45,000 fruits. After the parasites had become well established the fly population was reduced through parasitism to such an extent that the large numbers of fruits collected would yield barely enough larvae for a record of parasitization. This area is the only one in the islands where the Mediterranean fruitfly can be considered under control by parasites.

Table 5.—Parasitization of the Mediterranean fruitfly in coffee in the Kona district, Island of Hawaii, 1914–33

			Parasitiz	ation by-	_			Parasitization by—				
Year	Host larvae	Opius humilis	Opius tryoni	Opius fulla- wayi	Total parasi- tization	Year	Host larvae	Opius humilis	Opius tryoni	Opius fulla- wayi	Total parasitization	
1914 1915 1916 1917 1918 1922 1923 1924	Number 2, 830 4, 989 2, 382 4, 000 1, 510 428 256 126	Percent 41. 8 59. 4 55. 7 52. 4 12. 0 . 5 0 1. 6	Percent 3. 7 15. 2 22. 3 31. 2 70. 5 11. 4 25. 4 24. 6	Percent 0 3.8 2.4 8.7 78.5 55.1 48.4	Percent 45. 5 74. 6 81. 8 86. 0 91. 2 90. 4 80. 5 74. 6	1926 1927 1928 1929 1931 1932 1933	Number 111 484 131 161 477 244 124	Percent 0 . 4 0 0 0 0 0 0 0 0 0	Percent 18. 0 19. 6 7. 6 20. 5 51. 4 50. 0 79. 8	Percent 27.9 57.6 77.1 48.4 27.7 29.9 14.6	Percent 45. 9 77. 6 84. 7 68. 9 79. 1 79. 9 94. 4	

Opius humilis was first liberated in the Kona district in June 1913, when a few adults were placed under a tent covering a coffee tree

bearing infested fruits. Subsequent liberations were made, but the first colony increased in size from the beginning. The rapid increase in numbers of this parasite immediately following its liberation is indicated in the third column of table 5. During 1914, the first year after liberation, it parasitized 41.8 percent of larvae in coffee cherries collected during that year. During 1915, the second year after liberation, its parasitization increased to 59.4 percent, the maximum for the entire period. Beginning in 1916 the suppressing influence of the other two species of Opius, one of which had been liberated about a year after O. humilis, began to affect its development, and as these two increased in numbers and effectiveness parasitization by O. humilis decreased. During the period 1922-27, only a few adults of this parasite were reared from larvae held for parasite records. From 1928 to 1933, inclusive, not one adult of O. humilis was reared from larvae in coffee from Kona. These records furnish a striking example of the influence of one parasite on the development of another when both attack the same stage of the host. In the case of the fruitfly in Kona coffee its susceptibility to heavy parasitization has resulted in sufficient multiple parasitization to eliminate O. humilis as a control factor of the fruitfly in coffee in that district.

The first liberation of Opius tryoni in the Kona district was made in June 1913, at the same time that O. humilis was liberated. The records in table 5 indicate that it was slower than humilis in becoming established. It did not supersede humilis as the most effective parasite until 1918, 5 years after its liberation. The first liberation of O. fullawayi in this area was made late in 1914, and the insect reached its maximum of efficiency as a parasite 8 years later, in 1922. During the period 1922-29, fullawayi parasitized a higher percentage of larvae in coffee in Kona than humilis and tryoni combined. For some reason, the parasitization by fullawayi then began to decrease, and during the 3 years 1931-33 tryoni was more effective than fullawayi, and humilis had disappeared from the records. No reason is apparent for the rapid increase of tryoni over fullawayi. The outstanding points of interest in table 5 are the apparent elimination of humilis as a factor in the control of the Mediterranean fruitfly in coffee in that district, the high percentages of parasitization by fullawayi, and the high degree of control of the fly by parasites, which

amounted to over 90 percent in some years.

RECORDS OF INFESTATION

During the period 1916-33, the average number of larvae per fruit has been recorded for each variety of fruit collected. These records have been made to show any increase or decrease in numbers of Ceratitis capitata in Hawaii. All fruits collected for recording parasitization were counted and held until all larvae had emerged. The number of fruits and the number of larvae they contained were used as a basis for determining the average number of larvae per fruit. It is believed that these records, kept over a series of years and obtained from large numbers of fruits collected at frequent intervals throughout the year, furnish a reliable index of the changes in Mediterranean fruitfly population from year to year. The average infestation per fruit, of the collections during the period 1916-24 has already been published (3, 4, 6, 8, 9, 10). Table 6 contains the same information for the period 1925-33, together with the average infesta-

tion per fruit for all fruits collected during the 9-year periods 1916–24 and 1925–33. The average infestation per fruit over the first 9-year period is used as a basis of comparison with average infestations over later yearly periods, to show variations in infestation. In the publications just referred to, a decrease in infestation is shown in the majority of host fruits during the last 3 of the 9 years 1916–24.

Average infestation per fruit, as shown in table 6, for each of the yearly periods 1925–33, shows a decrease in infestation in the majority of varieties of fruits for each of the years 1925–33 when compared with the general average for the entire 9-year period 1916–24. Leaving out those fruits that were collected only occasionally during the two 9-year periods, and making comparisons only on those fruits that were collected during at least 5 years out of each 9, the infestation per fruit for all varieties so collected was lower in 92.9 percent of the cases during 1925 than the average per fruit in the same varieties for the 9-year period 1916–24. Similarly, during the remaining 8 years, 1926–33, the percentages of fruit varieties having a lower average infestation were 100.0, 87.5, 100.0, 75.0, 57.1, 66.7, 92.9, and 73.3, respectively.

Table 6.—Average number of larvae of the Mediterranean fruitfly per fruit examined in Hawaii for each year of the period 1925-33, and for the 9-year periods 1916-24, and 1925-33

Host fruit	1925	1926	1927	1928	1929	1930	1931	1932	1933	1916- 24	1925– 33
Validation of the second of th	Num- ber	Num- ber	Num- ber	Num- ber	Num- ber	Num- ber	Num- ber	Num- ber	Num- ber	Num- ber	Num- ber
India-almond (Terminalia catap- pa)	3. 9 3. 2	2. 4 3. 0 . 1	3. 7 3. 4	3. 0 5. 8	5. 1 9. 3	5. 8 16. 6	2. 7 3. 1 . 7	3. 1 6. 9	3. 8 7. 4 . 04	7. 9 5. 9 . 4	3. 7 6. 5
Strawberry guava (Psidium cattleianum) Surinam-cherry (Eugenia uni-	1. 2	. 2	.8		1. 6	1. 7	.1		.1	1. 5	. 9
flora)Satinleaf (Chrysophyllum olivae- forme)	. 9	. 5	.5	.8	. 9 6. 7	1. 2	. 5	. 6	. 5	1. 2	6.7
Malabar-plum (Rose apple) (Caryophyllus jambos) West Indian medlar (Mimusops	2. 6	3. 1	1.7	5. 2	3. 0	7.6	5. 5	4.1	5. 2	9.9	5. 4
elengi)	6.8	2.6	5.6	2. 3	. 2	5. 7 . 2	2. 1 . 01	2. 6	3.0	3. 7 . 6	3.1
folia)	1. 6 1. 1 6. 6	1. 8 1. 2 3. 4	2. 7 . 9 . 8 3. 7	1. 2 1. 2 1. 2 6. 4	3. 6 1. 6 1. 4 6. 1	5. 7 1. 2 6. 6	1. 3 2. 5 1. 7 4. 2	2. 0 1. 6 4. 7	1. 4 1. 8 2. 0 5. 9	4. 0 2. 4 2. 4 8. 2 3. 0	2. 5 1. 3 1. 2 4. 9 3. 0
Orange (Citrus aurantium) Tangerine (Citrus nobilis deli- ciosa) Lime (Citrus aurantifolia) Noronhia emarginata	2. 3 . 5 . 2 . 6	1. 3 1. 1 . 4 . 7	3. 6 1. 1 . 3 1. 0	.8	2.3	1.9 2.9 .1 .5	3. 5 3. 2 . 01	2. 3 1. 1 . 7 1. 2	6. 4 2. 9 . 2 2. 4	1. 5 . 6 1. 6	1. 8 . 3 1. 4
Ochrosia elliptica	1. 0 5. 1 2. 7	1. 0	1. 8 	1. 9	9. 9	1.1	. 9 4. 8 	1.4	.02	3. 7 3. 5 18. 4 5. 9	1.9 5.1 4.4
Star-apple (Chrysophyllum caini- to)	3.0		5. 3	. 8	2. 6	5. 7	2, 5	3.8	1. 1	0	. 3
ferum)	. 9 5. 1	1. 1 1. 5 1. 5 2. 3	. 2	.1	2.7	. 01 2. 0 . 6 . 2	. 03 -3. 2 -1. 0	2. 0	. 3 1. 6 1. 3	. 5 . 3 5. 1	.1 .9 2.2 1.0 1.4
Blucrown passionflower (passion fruit) (Passiflora caerulea) ————————————————————————————————————				.1	. 01	2. 6	3.4		.7		. 1 2. 1
Breadfruit (Artocarpus incisa)						.4		0			. 1

The decrease in fruitfly infestation is also shown by a comparison of the average infestation per fruit in fruits collected over the 9-year period 1916-24, with the average in those for the 9-year period Table 6 gives the average infestation as less during the latter period in 81.2 percent of the varieties of host fruits collected during at least 5 years of each 9-year period. While introduced parasites are an important factor in decreasing the numbers of the Mediterranean fruitfly in Hawaii, there are probably other reasons for the considerable decrease in host population during the latter of the two 9-year periods shown in table 6. The tendency of some insect pests in a new environment to spread rapidly and do heavy damage during the first few years after their introduction, and later to decrease in numbers, is well known. The decrease of the fruitfly on the island of Oahu may be partially due to this general tendency. The majority of fruits from which larvae were secured for the records in this paper were collected within the city of Honolulu. During the 20-year period covered the population of the city has more than doubled, resulting in the destruction of large numbers of fruit-bearing trees and shrubs to make way for additional buildings. This decrease in host fruits of the Mediterranean fruitfly may have been one of the causes of the decrease in infestation that is indicated by the records in

The data in table 7, covering the years 1916-33, show the total number of fruits of all varieties collected each year, the total number of larvae of the Mediterranean fruitfly obtained from these fruits, and the average infestation per fruit based on all fruits collected regardless of variety. This table is presented to show the number of fruits and fruitfly larvae used in recording the data in this circular, and to indicate variations in abundance of the fly through infestation aver-The average infestation per fruit, as computed in this table, indicates 1921 as the year of maximum fruitfly population during the period, and 1927 as the year when the fly was least abundant. averages of infestation during the second 9-year period show a considerable decrease over those in the first 9 years. This decrease corresponds with the results shown in table 6, where the average infestation per fruit for fruits of each variety was considered. It will be noted that the average yearly infestation for each year during the first 8 years of the period is above the average for the entire period in all but 1 year. During the last 10 years it is below the grand average each year excepting for 1929 and 1930. For 1930 a decided increase in infestation is shown as compared with the 7 preceding years and the 3 following years.

Figure 3 is presented to show the relationship, if any, between the total percentages of parasitization and the yearly average infestation per fruit over the 18-year period 1916–33, and is based on data in tables 2 and 7. During 8 years the graph shows decreases in the average infestation per fruit when the percentages of parasitization increased, or vice versa. This relationship is most evident in 1917, 1919, and 1930. In 1930 a very marked peak in the average infestation per fruit occurred, and this was accompanied by the lowest percentage of parasitization of any year during the entire period. This relation was not true during 9 years of the period, particularly in 1921 and 1929.

Table 7.—Average infestation per fruit by the Mediterranean fruitfly, in all fruits collected in Hawaii, during 1916-33

Year	Host fruits	Fruitfly larvae	Average larvae per fruit	Year	Host fruits	Fruitfly larvae	Average larvae per fruit
1916. 1917. 1918. 1919. 1920. 1921. 1922. 1922. 1923. 1924. 1925.	Number 117, 537 139, 345 151, 994 123, 856 128, 484 133, 646 106, 998 94, 583 92, 793 79, 585	Number 372, 655 350, 142 451, 319 522, 153 452, 187 677, 575 444, 986 294, 593 238, 691 167, 762	Number 3. 2 2. 5 3. 0 4. 2 3. 5 5. 1 4. 2 3. 1 2. 6 2. 1	1926	Number 95, 543 145, 372 88, 450 60, 770 57, 312 67, 550 64, 442 80, 858 1, 829, 118	Number 123, 108 155, 250 116, 981 178, 379 227, 941 131, 694 113, 487 165, 545 5, 184, 448	Number 1.3 1.1 1.3 2.9 4.0 1.9 1.8 2.0

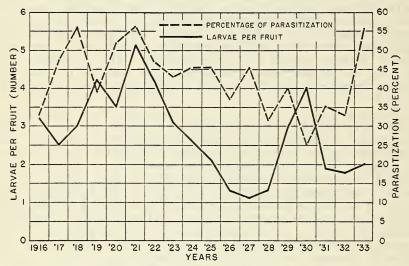


FIGURE 3.—Comparison of the percentage of parasitization with the number of larvae of the Mediterranean fruitfly per fruit in Hawaii from 1916 to 1933.

SUMMARY

The Mediterranean fruitfly was discovered in Hawaii in 1910. It encountered few natural enemies in its new environment until 1913 and 1914, when parasite introductions were made. The following four species of larval parasites became established: Opius humilis, O. tryoni, O. fullawayi, and Tetrastichus giffardianus. Records of parasitization by these parasites over the 20-year period 1914–33, and of the amount of infestation by the fruitfly from 1916 to 1933 made by the Bureau of Entomology, United States Department of Agriculture, are recorded in this circular.

Parasitization of larvae in some of the more favorable host fruits is shown to be high, often ranging between 95 and 100 percent in certain samples; but parasitization of larvae from all host fruits collected over yearly periods after 1914 ranged from 24.9 to 55.8 percent, with an average of 42.3 percent for the entire period. After liberation in Hawaii, Opius humilis became established and effective more rapidly than either of the other two species of Opius and became abundant 2 or 3 years sooner; but was soon superseded in effectiveness by

O. tryoni. Parasitization records, showing the efficiency of each species of parasite over monthly and yearly periods, indicate clearly the controlling influence of O. tryoni over O. humilis.

The texture of the skin and the thickness of the pulp of the various host fruits seems to be a governing factor in the degree of parasitization by Opius by rendering fruitfly larvae less accessible to the parasites in certain fruits.

The high degree of multiple parasitization of larvae in coffee cherries (coffee berries) in the Kona district on the island of Hawaii has eliminated O. humilis as a control factor of the Mediterranean fruitfly in that district, its place being taken by the other two species of Opius. This is the only section in Hawaii where the Mediterranean fruitfly can be considered under control as a result of introduced parasites. This control is due to the very high degree of parasitization of the fly in coffee cherries.

Of the four species of introduced parasites, Opius tryoni was the most valuable in controlling this fruitfly under Hawaiian conditions. O. fullawayi has ceased to parasitize larvae in nearly all fruits except

coffee cherries.

Data showing the average infestation per fruit over yearly periods, 1916-33, show a marked decrease in infestation during the last 10 or 11 years of that period. This decrease on the island of Oahu, although due largely to parasitic control, was to some extent, at least, caused by other environmental factors affecting the fly.

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18



